

VARIATION IN THE *ZOILA FRIENDI* (GRAY) SPECIES COMPLEX (GASTROPODA: CYPRAEIDAE) IN SOUTH-WESTERN AUSTRALIA

By BARRY R. WILSON* and RAY SUMMERS†

Pls. 1-4, text figs. 1-4.

Extreme intra-specific morphological variation is well known among terrestrial and freshwater mollusks (*e.g.*, Welch 1938, Diver 1939, Cain and Sheppard 1950, Leloup 1950, 1953) and several examples of such variation in marine species have been described (*e.g.*, McMichael 1959, Kincaid 1957). Griffiths (1962a) and Orr (1959) have shown that variation of this kind occurs in some species of the family Cypraeidae.

In this paper data are presented illustrating variation of several morphological characters of the *Zoila friendi* (Gray, 1831) species complex in South-western Australia. Representatives of the group are found along the continental shelf from Shark Bay on the mid-west coast of Western Australia to South Australia. Over much of this range they inhabit the full width of the continental shelf, but no specimens appear to have been collected from the outer part of the shelf in South Australia.

Within this unusually variable species complex previous authors have recognized two species each containing two subspecies (= races). A brief outline of this arrangement, and the previously stated diagnoses, is given below. This is followed by a consideration of the variation of each of the shell characters used by other authors to diagnose the "species" and "subspecies", plus our data on animal colour, radula and habitat. The value of these variants as systematic characters is discussed. It is shown that most of the shell characters previously used as diagnostic are not satisfactory taxonomic criteria. The taxonomy of the group is revised.

We use the generic name *Zoila*, with hesitations in view of the conclusions reached by Kay (1960). The anatomy of *Z. friendi* will be described and the problem of generic relationship will be discussed in a later paper.

PREVIOUS NOMENCLATURE

Zoila friendi friendi (Gray, 1831).

Diagnosis by previous authors: This western "subspecies" has been characterized by an elongate shell with elevated spire and upturned extremities (*i.e.*, produced sides of the anterior and posterior channels). The base of the shell is uniformly dark brown, the colour extending on to the sides from the base. The primary colour of the dorsum is pale cream with four radial bands of ash-blue blocks. This is partially obscured by varying degrees of irregular brown blotching. Some shells are almost uniformly dark brown on the dorsum as well as on the base and sides, *i.e.*, the underlying cream and ash-blue bands are completely covered.

Characteristically the teeth on the columellar side are reduced to several relatively strong anterior teeth and a few crenulations. There are no teeth or crenulations on the posterior half of the columella. The columellar teeth do not extend into the fossula. Schilder and Schilder (1938-39) give the formula $(73 \text{ [mean length]} \cdot 54 \text{ [mean width: length]} \cdot 18 \text{ [mean number labial teeth]} \cdot 15 \text{ [mean number columellar teeth]})$ for this race, and the range as "Swan River to Ellenbrook [approximately 20 miles south of Cape Naturaliste]".

* Curator of Molluscs, Western Australian Museum, Perth.

† P.O. Box 124, Petulama, California.

Zoila friendi vercoi (Schilder, 1930).

Diagnosis by previous authors: Verco (1918) described three wide specimens of *Z. friendi* from Esperance on the south coast of Western Australia. Schilder (1930) repeated Verco's description and gave them the racial name *vercoi*, designating Verco's specimens as types. Schilder did not personally examine these specimens.

A translation of Schilder's description is here given:

"*Zoila friendii vercoi* nov. subsp., when compared with *friendii* Gray s. str. (south west coast), is longer (81-94 mm. instead of 65-88, extreme range 42-88 mm.), broader (BL. [*i.e.*, Width: Length] = 56-62 instead of 52-55)¹⁷ and higher (HL. [*i.e.*, Height: Length] = 43-49 instead of 42-43); it differs from *thersites* Gaskoin (mid-south coast of Australia) in the base which is continuously black-brown up to the aperture. Furthermore, *thersites* is usually smaller (71-75, extreme range 65-83 mm.) and still broader (BL. = 66-69) and higher (HL. = 52-55)."

"(¹⁷ For the relative breadth and height index only the 50% limits are given, for absolute length the extreme range is given in addition.)"

In a later paper Schilder and Schilder (1938-39) added "... besides the aperture of *vercoi* is wider, and the spire is said to be less projecting than in *friendii* but more than in *thersites*" but noted that the race needed confirmation. They give the formula (85.60.?.?).

Zoila thersites thersites (Gaskoin, 1849).

Diagnosis by previous authors: Shells from Port Lincoln to Beachport, South Australia, are relatively wider than those from Esperance, and were supposed to have an even shorter spire and less turned up extremities. The colour pattern of the dorsum and sides as in *Z. friendi*, but the dark brown on the base does not extend all the way to the edges of the aperture. Schilder and Schilder (1938-39) give the formula (74.68.17.14) and the range Port Lincoln to Beachport, eastern South Australia.

The systematic status of these South Australian populations has always been controversial. Verco (1918) placed them as a race of *Z. friendi*. Schilder and Schilder (1938-39) used this interpretation but in a more recent paper (1961) follow most recent authors and list *thersites* and *friendi* as distinct species.

Zoila thersites contraria (Iredale, 1935).

Diagnosis by previous authors: Verco (1912) recorded pale *Z. thersites* dredged from 72 to 100 fathoms in the western part of the Great Australian Bight. Iredale (1935) recognized these as a distinct subspecies but did not give adequate diagnosis. He gave no reasons for regarding these shells as pale forms of *Z. thersites* rather than of *Z. friendi*. Presumably he was influenced by the fact that the deep water pale shells are as wide or wider than *Z. thersites*. They differ from both "species" in the general loss of dark shell pigment. Usually remnants of the colour pattern remain as pale orange marks, but in some specimens the shell is entirely white or off-white. Schilder and Schilder (1938-39) give the formula (70.68.18.13) for this race. Griffiths (1962b) recognizes *Z. contraria* as a full species.

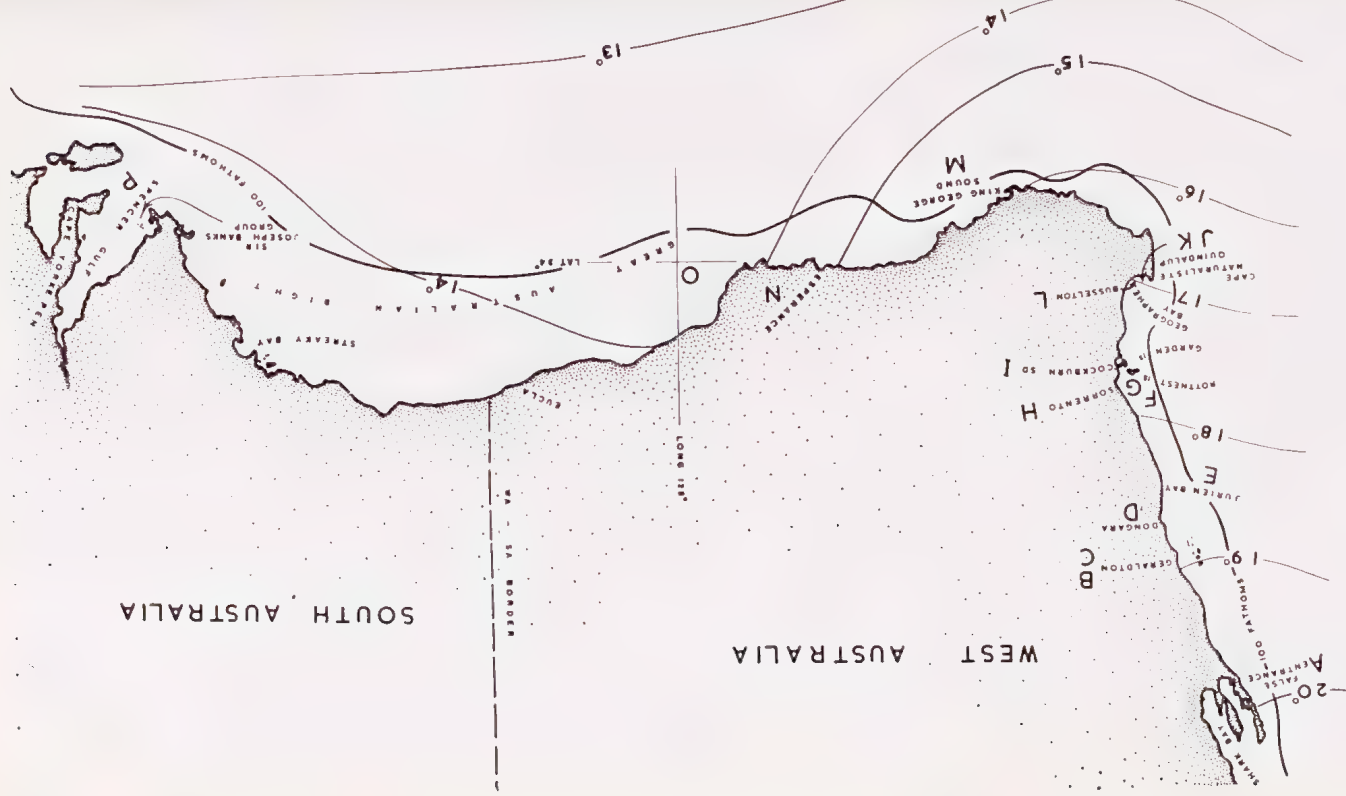
In addition to the four "subspecies" listed above *Z. marginata* Gaskoin 1848 and *Z. venusta* Sowerby 1859 (= *Z. episema* Iredale 1939) have at times been placed as subspecies or synonyms of either *Z. friendi* or *Z. thersites*. These are now generally accepted as quite distinct species, an opinion with which we entirely agree, and we do not propose to consider them in the present paper.

HABITAT AND DEVELOPMENT

In shallow water in Western Australia *Z. friendi* occurs among meadows of the sea-grass *Posidonia*. They may be found perched up on *Pinna* shells, sponges, sponge covered rocks or on jetty piles. Mr. Paul Trenberth (1962 and personal communication) takes *thersites* on sponges in 2 to 4 fathoms in the vicinity of the Sir Joseph Banks Group, Yorke Peninsula, South Australia.

The *Posidonia* meadows do not extend far below 10 fathoms off the Western Australian coast. Little is known about the habitat of *Z. friendi* below this depth although a close association with sponges seems certain. One specimen was collected by a diver in 17 fathoms off Rottnest Island from a sponge on limestone rock. Other deep water specimens have been taken from "crayfish" pots (with hermit crabs) or dredged.

Trenberth (1962) records egg-sitting females of *thersites* in South Australia in October to January. In Cockburn Sound during the early summer (October to January) females may be found "sitting" on eggs. The egg clutch is a compact mass 5 to 6 cm. in diameter with 4 to 5 layers of egg capsules at the centre. There are between one and two hundred capsules per clutch, each capsule being about 2.5 mm. in diameter. The egg masses are orange and are generally laid in depressions in sponges or dead bivalve shells. Mrs. S. Slack-Smith advises us that an egg mass collected in Cockburn Sound in late October, 1964, contained tiny transparent shells of about one whorl. The females sit over their clutch completely covering it and will return to this position if disturbed. Whether the females remains there until the larvae hatch is uncertain. Further study is also required before it can be determined whether these cypraeids have a short planktonic larval stage, or whether development is direct. Ostergaard (1950) showed that Hawaiian cowries he studied have short pelagic stages. Griffiths (1962a) concluded that development is direct in species of the southern Australian group assigned to the genus *Notocypraea*.



Text fig. 1. Map of the area showing sample localities (see table 1).

VARIATION OF SYSTEMATIC CHARACTERS WITHIN THE *Z. FRIENDI* COMPLEX

(1) *Shell dimensions and proportions*: Shells collected near limestone reefs in open ocean water off Sorrento Beach, approximately 20 miles north of Fremantle, are consistently larger than shells from Cockburn Sound about 25 miles further south where the environment is more sheltered and almost land locked by Garden and Carnac Islands. We have seven specimens from Sorrento ranging from 85 to 99 mm. in length (mean 91 mm.). The mean of our Cockburn Sound sample is 72 mm. and the largest shell 83.8 mm. A similar situation is seen in Geographe Bay, where adult shells collected from a small, shallow water population cut off from the open ocean by a wide, shallow sand bar, are consistently very small (mean length 50.8 mm.) while shells from outside the bar in more open water are much larger (mean length 75.5 mm.).

Such inter-locality variation in overall shell size appears to be common throughout the range of the species complex and is almost certainly eco-phenotypic. Total length is thus a most unsuitable systematic character. It is significant that in both instances described above there is no significant difference in the relative width:length proportions of the shells in our samples from adjacent populations, despite the large differences in overall size.

Relative width is the main character that has been used to separate the four races. Verco (1918:147) stated that there is an "uninterrupted gradation" in the increase in relative width from Fremantle to South Australia. Our data based on much larger series confirms this for shallow water populations in Cockburn Sound, Geographe Bay, Esperance and South Australia. The ranges in relative width of all four major samples overlap considerably and there is no apparent sudden change at any point. This character seems to be purely clinal. However, the rate of increase in relative width is not constant over the whole length of the cline. The most rapid increase takes place down the west coast southwards from Cockburn Sound. Eastwards from Cape Leeuwin the rate of increase is much less. Plotting relative width (W:L) against distance, the means fall in a curve rather than a straight line (fig. 2).

Specimens from deeper water do not follow this trend for they invariably have a greater relative width than shells from adjacent shallower water, i.e., there is also clinal increase in relative width with increasing depth. The mean W:L ratio of our Cockburn Sound sample is 0.521. One specimen from 17 fathoms off Rottne Island has a W:L ratio of 0.606, and another (a pale shell) from "80-100 fathoms between Fremantle and Geraldton" has a ratio of 0.636. Other specimens from deep water north of Fremantle show the same trend (table 1).

An increase in relative width with increasing depth is also supported by data from the south coast. The mean W:L ratio of our small King George Sound sample is 0.665 and falls well above the mean curve for shallow water shells. Two of the seven shells in this sample were trawled in 25 fathoms. The remaining specimens were collected on the beach at Frenchman's Bay near the mouth of King George Sound and the depth from which they originally came is unknown. However, it is reasonable to suspect that they came from moderately deep water as the coast line at this locality shelves steeply into 17 fathoms or more. The mean W:L of the sample of the pale shells ("*contraria*") from 60-100 fathoms in the western part of the Great Australian Bight also falls well above the mean curve for the shallow water shells in that region.

In fig. 2, both W:L ratio and winter surface water temperature are

plotted against distance along the coast. The resulting curves are similar which suggest that water temperature may be the environmental factor producing the clinal increase in relative width. Unfortunately hydrological data are poor for this region, but it is probable that there is a similar decrease in bottom water temperature across the continental shelf from the coastal shallows down to the edge of the continental slope.

Disregarding other characters, these data could be interpreted as demonstrating that all the shells belong to the one species in which there is clinal increase in relative width in two planes: horizontally from north to south and east, and vertically from the coast line down to the outer edge of the continental shelf. According to this interpretation the same cline operates along all contour levels around the shelf, but with the deeper levels "in advance" of the inshore shallow water cline. This idea is represented diagrammatically in fig. 2 (inset).

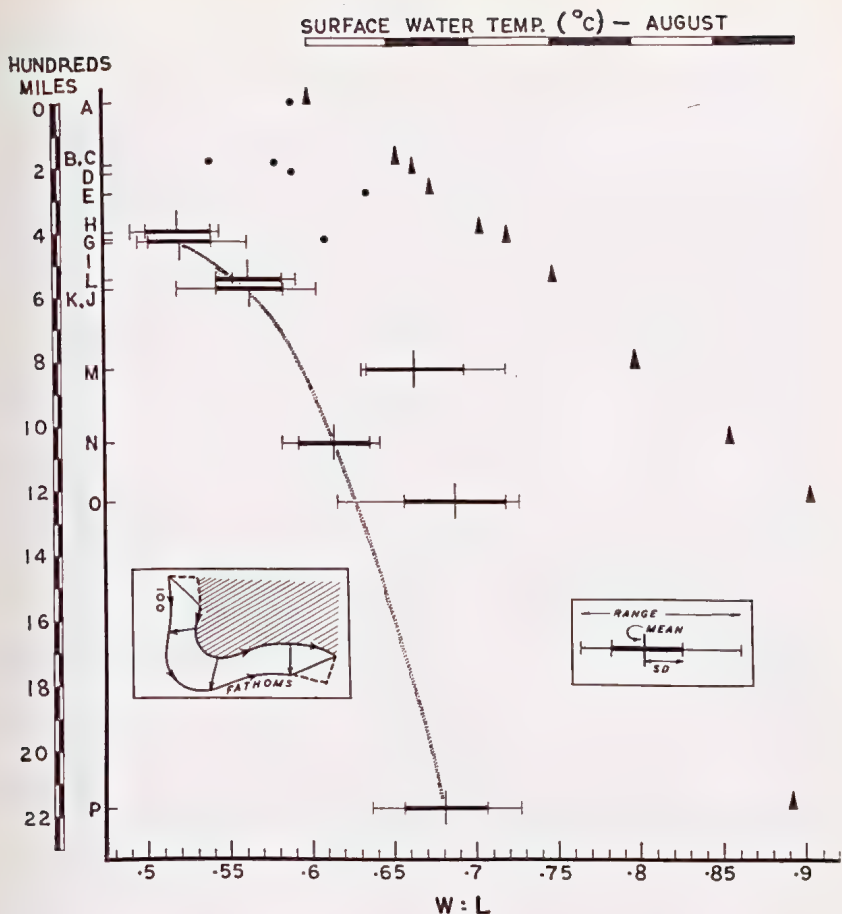
Our interpretation gains indirect support from the coefficients of variation calculated for all samples (table 1). The King George Sound and Great Australian Bight samples, both heterogeneous in respect to depth of collection, have a significantly higher variability than the four samples from shallow water which are comparatively homogeneous in this respect. If relative width increases with increasing depth such variability would be expected in samples taken from a wide range of depths.

Relative width is thus an unsuitable criterion for separating species or subspecies in this complex, since its variation appears to be continuous with no evidence of any sudden change at any point to indicate regions of restricted gene flow. Use of this character would be impossible in any case without knowledge of locality and depth because of the overlap in statistical range. The mean of the King George Sound sample is less than one standard deviation from the mean of the South Australian sample. One specimen from King George Sound, recently examined by Schilder and identified as *Z. friendi vercoi* (West Australian Museum regn. no. N1996), has a W:L ratio of 0.702 compared with 0.681, the mean of the South Australian sample.

(2) *Spire position and height*: In shells from the Fremantle area and northwards the spire invariably lies to the left of the posterior channel. This is exceptionally pronounced in specimens from Sorrento Beach. In most Geographe Bay and King George Sound shells the spire is similarly positioned, but in an occasional specimen the spire apex falls within the posterior channel (e.g., pl. 1, fig. g). A little under 50% of the Esperance specimens have the spire apex lying to the left of the posterior channel; in the remainder it lies within, and this appears to be the invariable rule for South Australian shells.

There is therefore a progressive shift in the position of the spire apex in relation to the posterior channel, from north-western populations to south-eastern populations. This shift appears to be related to relative width, as those specimens from intermediate localities in which the spire apex falls within the posterior channel are invariably the widest specimens in the samples. Generally the wider and more gibbous the shell the more the aperture is curved and the posterior channel deflected to the left to encompass the spire apex.

We have measured spire height diagonally from the most dorsal point of the last suture to the apex and expressed it as a percentage of aperture length (i.e., distance between inner edges of anterior and posterior channels). The results are graphed in text fig. 3a. It is clear that this character is also clinal and is probably directly related to relative width.



Text fig. 2. Relative width and mean surface water temperature (August) plotted against distance in miles from the most northern locality (Shark Bay), showing clinal increase in relative width from north to southeast of samples from shallow water (*i.e.*, samples H, I, L, K, J, N, P) and the corresponding decrease in surface water temperature. Samples from deeper water (*i.e.*, samples A, B, C, D, E, G, M, O) fall above the curve drawn between means of shallow water samples.

Inset illustrates the known distribution of the species on the continental shelf and the directions of the clinal increase in relative width (*i.e.*, horizontal and vertical).

TABLE 1

Locality	Sample code	Depth in fathoms	Total sample number	Register numbers of specimens in museum collections
False Entrance	A	25	1	WAM: 67-62
Off Geraldton	B-C	20-25	2	WAM: 8/9-62
Off Dongara	D	32	1	WAM: 7-63
"Between Fremantle and Geraldton"	E	80-100	1	WAM: 4999
20 miles NW Rottne Id.	F	85-110	fragments	WAM: 30-63
1 mile N Bathurst Light, Rottne Id.	G	17	1	WAM: 68-62
Sorrento	H	2-3	7	
Parmelia Bank, Cockburn Sound	I	1-4		WAM: 35/36-62; 10/12-63
Geographe Bay—off Quindalup	J	2-8	26	WAM: 38/54-62; 13/23-63
Geographe Bay—inside sand bar, Quindalup	K	0-1	16	WAM: 1-62; 55-62; 24-63; N2465
Geographe Bay—Busselton jetty	L	2-3	10	WAM: 25/28-63
King George Sound	M	?	6	
Esperance	N	2-4	9	WAM: 29-63
Western part of Great Australian Bight	O	70-100	28	WAM: N1996; 57/58-62
			21	WAM: 69/79-63; 37-62; 56-62
Spencer Gulf, South Australia	P	1-4	26	WAM: 3-62 NMV: F12900; F22860(2); F20883(2); F2508; F22863 AM: C35580; E3839; E3848 WAM: 130/131-45; 59/61-62 NMV: F1375; F17708(9); F22864(4); F22861; F16468; F2334(3); F22862(2)

TABLE 1. *Material examined.* Localities are indicated on text fig. 1 by sample code letters. Specimens examined in private collections are included in the total sample number (and were used in calculations), but the register numbers of only those specimens permanently lodged in museum collections are given. WAM = Western Australian Museum [Perth]; NMV = National Museum of Victoria [Melbourne]; AM = Australian Museum [Sydney].

(3) *Aperture width*: Verco (1918: 147) noted that: "The width of the aperture is not diagnostic. This is as narrow in the extreme western form as in the extreme eastern, while in the Esperance specimens it is wider."

Our measure was taken from the interstices between the labial teeth to the columellar callus, at the point where the shell was widest, and expressed as a percentage of total shell width. Relative aperture width is greatest in the King George Sound sample and decreases progressively in samples from the north and east of this (text fig. 3b). This progressive decrease may be coincidental, or it may be interpreted as clinal decrease in either direction from a central point. In the former case aperture width would be diagnostic of local populations only and have no systematic significance. Neither could this character be used as a systematic criterion if it varies clinally. In any case, the mean relative aperture width of our sample from Geographe Bay is greater than that of the Esperance sample. Clearly the use of this character to diagnose Esperance shells as a distinct subspecies is untenable.

(4) *Extremities*: One of the most striking features of west coast *Z. friendi* is the produced and turned up sides of the posterior and anterior channels. This is frequently used as a diagnostic character of this western "subspecies" (e.g., Allan, 1956). Our measure was aperture length subtracted from total length, as a percentage of total length. Only fully mature shells were used as this is an adult characteristic. Text fig. 3c shows that the statistical ranges of all samples overlap and there is no apparent pattern of variation. The means of the Esperance and Sorrento samples are both significantly greater than the mean of the Cockburn Sound sample. Use of this character to separate west coast populations from southern populations is erroneous.

(5) *Dentition*: The "reduced number" of labial teeth have been calculated using Schilder's formula (Schilder and Schilder, 1938-39). There is no significant difference between samples from Cockburn Sound, Sorrento, outer Geographe Bay, King George Sound, Esperance, Great Australian Bight and South Australia. In every case the average reduced number is about 17. (The Schilders give 17 for *Z. friendi friendi* and *Z. thersites contraria*, and 18 for *Z. thersites*.) The sample of dwarf shells from inside the sand bank in Geographe Bay has an average reduced number of 15. This may be interpreted as a local variant.

The columellar teeth are variable and difficult to count accurately and consistently. The first 4 to 8 teeth at the anterior end are usually strong, but never extend down on to the fossula. Behind these the columellar teeth rapidly become weak and reduced to mere crenulations. In shells from Cockburn Sound, Sorrento, Geographe Bay, King George Sound, Esperance and the Great Australian Bight there is rarely any sign of crenulations on the posterior half of the columella. However, in South Australian shells there are frequently 2 to 4 such crenulations at the posterior end. Sometimes these form relatively strong teeth. In occasional South Australian shells there are faint teeth all along the columella besides the usual 4 to 6 strong anterior teeth.

The four specimens from deeper water northwards from Fremantle all have faint teeth all along the columella, in addition to the usual few strong anterior teeth. This is particularly pronounced in the specimen from 20-30 fathoms off False Entrance in which there are 14 strong anterior teeth in a total of 31 (30 labial teeth). The tendency to retain the full complement of columellar teeth is therefore a feature of shells from the extreme limits of the species' geographic range.

TABLE 2. WIDTH: LENGTH STATISTICS FOR MAJOR SAMPLES.

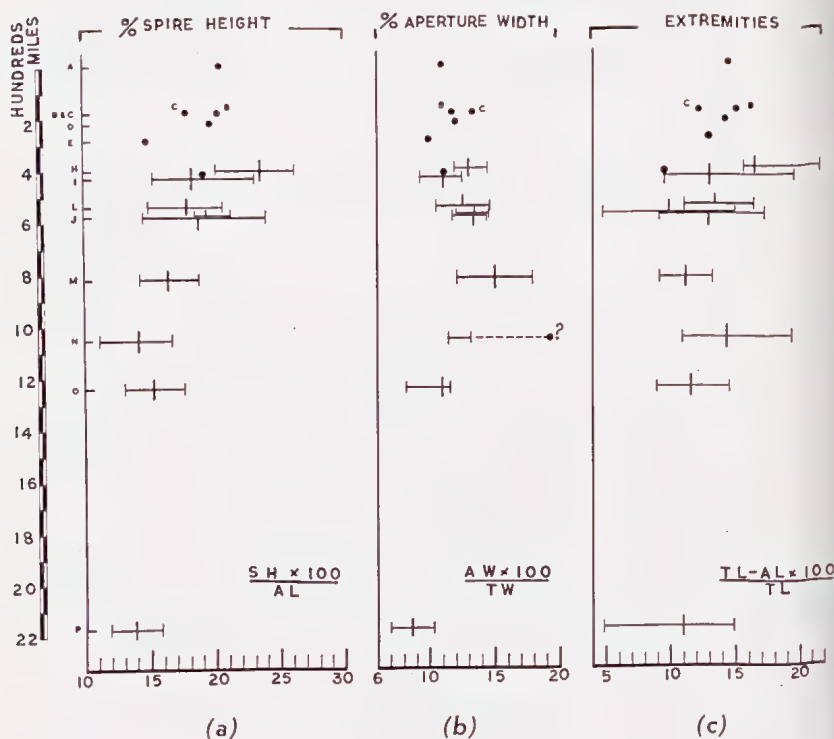
Locality	Mean	SD	V	N
Sorrento (H)	0.519	0.0178	3.43	7
Cockburn Sound (I)	0.021	0.0188	3.61	26
Geographe Bay (J + K + L)	0.565	0.0197	5.09	32
King George Sound (M)	0.665	0.0339	3.38	7
Esperance (N)	0.611	0.0208	4.63	28
Great Australian Bight (O)	0.700	0.0324	3.64	18
Spencer Gulf (P)	0.681	0.0248	3.43	26

Mean = sample mean

SD = one standard deviation

V = variance

N = sample number



In all samples there is variation in the thickness and strength of both the labial and columellar teeth. In the Esperance sample a number of specimens have quite fine teeth, *i.e.*, this population shows more variability in this respect than other populations sampled (pl. 2, cf. figs. f, g).

(6) *Radula*: One of us (BRW) has examined series of radulae of animals from Sorrento (2), Cockburn Sound (20), Geographe Bay (6), Esperance (10) and the Sir Joseph Banks Group, St. Vincent Gulf, South Australia (15).

The radula is typical of Cypraeinae in bearing 7 tricuspid teeth per row with 80 to 150 rows. The median tooth is slightly wider than it is high with one prominent medial cusp bordered by a smaller cusp on either side. An internal dumb-bell-shaped bract extending across the base of the tooth stains more densely (chlorazol black) than the remainder of the tooth and bears a pair of small denticles, one in each lower corner. A prominent semi-circular bract, which does not take up the stain, projects downward from the base of the medial tooth. This latter element appears to be the structure Kay (1960) calls the "sub-tending bract".

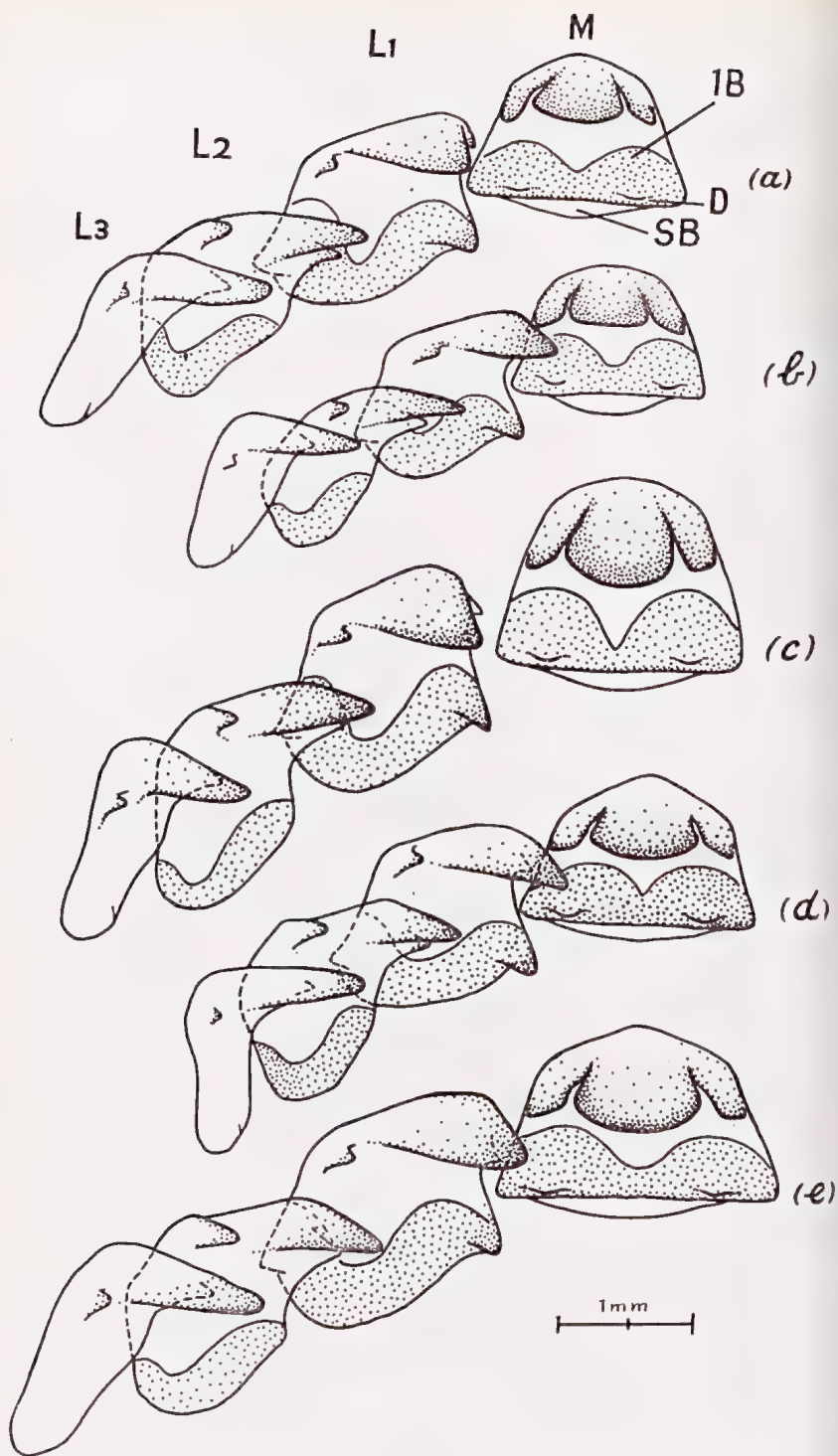
The first lateral tooth (= "admedian" of Kay) is slightly higher than it is wide. It possesses a prominent medial cusp which is large and pointed while the lateral cusps are relatively small. A densely staining internal bract also occurs in this tooth. Large denticles are present on the lower corners of the tooth, the one on the inner corner being particularly prominent and projecting toward the median tooth. The second lateral tooth is similar to the first but is narrower with a more prominent central cusp and does not possess basal denticles. The third (outer) lateral is narrower still, its lateral cusps are very reduced, no internal bract is visible, and there are no basal denticles.

The shape and proportions of the median tooth and the second lateral tooth vary slightly. The median tooth of South Australian and Esperance specimens tends to be lower and wider than that of west coast animals. There are indications that this may be clinal character. In South Australian and Esperance specimens the outer lateral cusp on the second lateral tooth forms a distinct shoulder. This is present but less distinct in Geographe Bay and Sorrento samples. The specimens from Cockburn Sound (text fig. 4b) are exceptional in that the second lateral tooth is relatively narrow and there is no shoulder at the outer lateral cusp. This is consistent in specimens from this locality but appears to be a local feature, not a regional one (cf. nearby Sorrento animals).

On the whole there is little variation in the radula in this species complex. The variants described above do not appear to provide any satisfactory basis for subdividing the group into races or species, although a more detailed biometric study may be necessary to be sure of this. It will be interesting to examine the radulae of pale shells from deep water when these become available.

Text fig. 3. Sample statistics of three shell characters plotted against distance in miles from the most northern locality (Shark Bay). Solid circles represent single specimens. For detailed sample and locality data see table 1.

TL = Total Length; TW = Total Width; AL = Aperture Length; AW = Aperture Width; SH = Spire Height.



(7) *Animal colour*: One of us (BRW) has studied living and preserved specimens from the Fremantle area, Geographe Bay, Esperance and South Australia. There is little intra-population variation in the colouring of the animal from any of these localities, and no evidence of any inter-population variation. The mantle, head, eye, tentacles, siphons, and sides of the foot are jet black. Mantle papillae are widely spaced and so small that they are barely visible in a fully extended living animal. The anterior end of the foot is truncated and the shallow groove along the leading edge is yellow. This yellow streak may sometimes extend about an inch back along the latero-ventral edges of the foot. The base of the foot is dark gray or black.

It would be interesting to know whether the animals living below 50 fathoms lack dark pigments in the soft parts as well as in the shell.

(8) *Shell colour*: It is important to distinguish between colour pattern and colour intensity.

(a) *Colour pattern*: In all specimens with any shell colour present the shells show the basic dorsal and lateral pattern as described above for shallow water west coast *Z. friendi*.

In most shells, except those from South Australia, the solid dark pigment on the base extends from the lateral callouses to the edges of the aperture (but not into the tooth interstices which are white). Invariably the base colour of South Australian shells does not reach the sides of the aperture, *i.e.*, the aperture is bounded by a white patch on each side (pl. 2, fig. j). By this character South Australian shells can always be recognized, and it seems to be a useful systematic criterion. However, several specimens in the Esperance sample show a slight loss of colour from the sides of the aperture. This suggests that there may be intergrades of this character between Esperance and South Australia in which case the character can have no systematic value. Specimens from intermedite localities are needed.

(b) *Colour intensity*: Specimens trawled from 70-100 fathoms in the western part of the Great Australian Bight (*i.e.*, specimens known as *Z. thersites contraria*) generally have the same basic pattern as shallow water *Z. friendi*, but there is a marked loss of the dark brown shell pigments. The underlying radial bands are either very pale orange or absent. The dorsal blotches are generally few and reduced to pale orange and the overlying pigmentaton of the sides is similarly reduced. The lateral spots are usually more obvious in these deep water shells as the density of the overlying pigments is less. In some shells all traces of colour pattern are lost and the shell is entirely off-white, but all intermediate stages are present in our sample.

It is significant that in all specimens from this area with some pigmentation of the base the colour extends from the lateral callouses to

Text fig. 4. Radulae of specimens from: (a) Sorrento (WAM 36-62); (b) Cockburn Sound (WAM 53-62); (c) Geographe Bay (WAM 1-62); (d) Esperance (WAM 73-62) and (e) Sir Joseph Banks Group, Spencer Gulf (WAM 61-62). Radulae stained with chlorazol black; stippling indicates density of stain.

M, medium tooth; L1-3, lateral teeth; IB, internal bract; D, denticle; SB, sub-tending bract.

the sides of the aperture. In this respect they resemble *Z. friendi* from Esperance and westward rather than South Australian shells.

There is a single specimen in the Western Australian Museum collection which was trawled by the "Endeavour" in 1912 "between Fremantle and Geraldton in 80-100 fathoms," with white sides, base and dorsum. The dorsum is slightly flecked with orange-gray spots. That this shell is correctly placed in the *Z. friendi* complex is supported by darker shells of similar shape from intermediate depths (e.g., pl. 1, fig. a). A recent dredging expedition by the Western Australian Museum produced many basal fragments of similar shells from 85-110 fathoms, approximately 20 miles N.N.W. off Rottnest Island, Western Australia. These fragments are all either white or pale orange, some with orange lateral spots. They were associated with a belt of white sponges and bryozoa.

There is great intra-locality variability in the shape, size and number of the dorsal blotches, but there appears to be little variation between shallow water populations from one end of the range to the other. However, there is a marked tendency for a decrease in the number of dorsal blotches in deep water shells; they may be absent in some specimens from the outer edge of the continental shelf (see below).

The radial bands are generally at least partially visible but may be obscured by the dorsal blotches in particularly dark shells. Similarly the large round lateral spots are generally present but are often obscured by the dense brown of the sides.

Thus it seems likely that a pale form of *Z. friendi* occurs all along the outer edge of the continental shelf off southwestern Australia. The specimen dredged by Verco (1912) in 72 fathoms in the Great Australian Bight is so far the shallowest record for the pale shells. In the same publication Verco records a dark specimen of *Z. thersites* dredged in 40 fathoms off Kangaroo Island, South Australia. There is a dark specimen in the Marwick (the late T. W. Marwick of Perth) collection from 40 fathoms in the Recherche Archipelago, and all other specimens examined from less than 40 fathoms in Western Australia are dark. The loss of colour must therefore begin between 40 and 70 fathoms.

This loss or reduction of shell colour intensity is almost certainly eco-phenotypic. It may be a direct or indirect result of decreased light. The shells of all other molluscs dredged from the white sponge belt off Rottnest were white or pale orange (even the filter feeding lamellibranchs) and it seems unlikely that the loss of the brown and blue pigments in *Z. friendi* is due solely to the lack of these pigments in their food (i.e., white sponges?). If the loss of pigment is a direct function of depth we should expect it to be clinal which appears to be the case.

DISCUSSION

Diagnostic characters used to separate subspecies or closely related species must be relatively consistent and characteristic of a geographical region not just a local population. They should be discontinuous. Clinal characters are useful in few circumstances, while eco-phenotypic and genetic variants restricted to local populations, or demes, are unacceptable as systematic characters.

Most of the characters examined in this study of the *Z. friendi* species complex show exceptional variation, either inter-locality, intra-locality or both. We have assigned each of these variants to one of the four categories listed below.

(i) *Intra-locality variants*: The number of dorsal blotches and position of the spire apex in relation to the posterior channel (Esperance population) are the most striking examples, but most characters show consider-

able variation within samples from a single locality. The degree of intra-population variation in the *Z. friendi* complex emphasizes the need for large series of specimens in similar studies.

(ii) *Inter-locality variants restricted to small localized demes (i.e., no geographical pattern)*: Overall size, amount of upturning of the anterior and posterior channel sides, and possibly aperture width, vary from one locality to another, apparently without any geographical pattern. Occasionally a single population may be characterized by a particular variant which elsewhere does not vary much at all, e.g., the shape of the second lateral radula tooth of Cockburn Sound animals; or which varies clinally over the remaining range of the species, e.g., the extreme offset spire of Sorrento animals.

Some of these random inter-locality variants are almost certainly eco-phenotypes, e.g., overall size, but other may have a genetic basis, possibly due to small size of the demes and lack of effective dispersal.

(iii) *Geographically continuous variants, i.e., clinal characters*: The two dimensional (horizontal and vertical) cline in relative width is a striking feature of this species complex. With it is associated position and height of the spire. Relative aperture width, shape of the central radula tooth and colour intensity may also be clinal.

(iv) *Geographically discontinuous variants*: The only characters which appear to fall within this category are the presence of posterior columellar teeth and base colour. South Australian shells may always be recognized by the white patch on each side of the aperture and generally by the presence of 1 to 4 posterior columellar teeth or crenulations. No other shell characters seem to be acceptable for the subdivision of the species complex into related species or races.

As far as is known to the authors no specimens have been collected between the western part of the Great Australian Bight and Streaky Bay in South Australia. This is a particularly inaccessible stretch of coast and, although this gap in the records may be due to a real absence of individuals there, it may be due to lack of collecting. Therefore we cannot discount the possibility that the two characters described above as discontinuous variants may also be clinal, with inter-grades between Esperance and Streaky Bay. On the other hand if there is a real gap in the species distribution in the central Bight area, then two allopatric systematic units may be recognized within the species complex. One of these units would extend across the full width of the continental shelf from Shark Bay to the western part of the Bight, and the other restricted to comparatively shallow water along the coast of South Australia. If this is so, then South Australian populations must receive some level of taxonomic recognition. A final decision must wait until an intensive search has been made along the shores of the central section of the Great Australian Bight.

Much of the inter-locality variation seen in this group is probably eco-phenotypic, some probably has a genetic basis which may be accounted for in part by restricted larval dispersal. In this respect the species may be compared with *Cymbiolacca pulchra* studied by McMichael (1959) and species of *Notocypraea* studied by Griffiths (1962a). However, the variation within the *Z. friendi* group is even more complicated by the strong clinal trends of some characters. That section of the Australian coastline between Shark Bay and South Australia is characterized by an absence of marked geographical barriers and by a slow gradient in surface water temperature (see text fig. 1). Clines should therefore be expected in species which are widely distributed along this coastal gradient.

The data presented here draw attention to the inadequacies of the

current nomenclature of the group and emphasize the need for great care in taxonomic studies of the Cypraeidae. Information on the biology and life history of cowries is urgently needed to provide background for such studies.

TAXONOMIC CONCLUSIONS

In the absence of specimens from localities in the Great Australian Bight, between Esperance and Streaky Bay, we propose provisionally to follow Verco (1918) and recognize only one species with two subspecies in this highly variable complex.

Zoila friendi friendi (Gray, 1831).

Cypraea friendii Gray, 1831, *Zool. Miscell.*, p. 35 (New Holland, near Swan River [type locality here restricted to Cockburn Sound and Owen Anchorage between Garden and Carnac Islands and the mainland]). Lectotype, selected by S. P. Dance, Brit. Mus. (N.H.), regn. no. 1964777.

Cypraea scottii Broderip, 1831 [July, 1832], *Zool. J.*, 5:330 (Strait of Sunda, near Angia, Java). Sowerby, 1837, corrected the locality to Garden Island, Swan River. Type not located.

Cypraea thersites Gaskoin. Verco, 1912, *Trans. Roy. Soc. S. Aust.*, 36:209-210 (in part, i.e., three specimens dredged from 78-100 fms. west of Eucla, Great Australian Bight).

Cypraea friendii friendii Gray. Verco, 1918, *Trans. Roy. Soc. S. Aust.* 42:144-145.

Zoila friendii vercoi Schilder, 1930, *Zool. Anz.*, Leipzig, 92:74 ("westliche Südküste von Australien; Typus: das mittelgrosse [South Aust. Mus. regn. no. D14124], von Verco 1918, *Trans. R. Soc. South Austr.*, Vol. 42, p. 147, erwähnte Stück von Esperance).

Zoila thersites contraria Iredale, 1935, *Aust. Zool.* 8:107 (72-100 fms. west of Eucla, Great Australian Bight). The types are the specimens collected by Verco (Verco, 1912). Lectotype, here selected, Australian Mus. Sydney regn. no. C35580; also two paralectotypes Australian Mus. regn. no. E3848 and E3839.

Zoila friendii friendii Gray. Schilder and Schilder, 1938-39, *Proc. Malac. Soc. Lond.* 23:174.

Zoila friendii contraria Iredale. Schilder and Schilder, 1938-39, *Proc. Malac. Soc. Lond.* 23:174.

Cypraea contraria Iredale. Griffiths, 1962, *the Cowry*, 1:36-38.

Range: Shark Bay to the western part of the Great Australian Bight at depths of a few fathoms to at least 110 fathoms.

Diagnosis: Shell colour varies from almost totally dark brown (some inshore shells) to entirely off-white (some deep water shells), but when any pigmentation of the base occurs it extends from the lateral callouses to the edges of the aperture. There are only 4 to 8 strong anterior columellar teeth and no posterior columellar teeth, although specimens at the northern end of the range possess faint crenulations all along the columella.

There is no evidence to support the status of Western Australian south coast populations as a distinct race of *Z. friendi*. The shell characters previously used to diagnose this supposed race (i.e., *vercoi*) are all either clinal or subject to non-geographical, inter-locality variation. The evidence presented in this paper clearly indicates that the deep water pale shells (i.e., *contraria*) are ecotypes of Western Australian *Z. friendi* and could not be regarded as a western race of *Z. thersites*, even if *thersites* were a valid species.

Zoila friendi thersites (Gaskoin, 1849).

Cypraea thersites Gaskoin, 1849, *Proc. Zool. Soc. Lond.* for 1848, 16:90 (Hab. ? [Roberts, 1885 [in], Tyron, Man. of Conch. gives South Australia]). Lectotype, selected by S. P. Dance, Brit. Mus. (N.H.) regn. no. 1846.5.15.1, bears no locality.

Cypraea friendii thersites Gaskoin. Verco, 1918, *Trans. Roy. Soc. S. Aust.*, 42:144-148.

Zoila thersites thersites Gaskoin. Iredale, 1935, *Aust. Zool.*, 8:107.

Zoila friendii thersites Gaskoin. Schilder and Schilder, 1938-39, *Proc. Malac. Soc. Lond.*, 23:174.

Zoila thersites Gaskoin. Schilder, 1961, *The Veliger*, 4:110.

Range: Streaky Bay to Beachport in South Australia down to depths of 40 fathoms.

Diagnosis: Differs from *Z. friendi friendi* in having a white patch on each side of the aperture. No deep water pale specimens are yet known. Generally there are 1 to 4 relatively strong teeth at the posterior end of the columella in addition to the usual 4 to 8 strong anterior columellar teeth. This eastern subspecies needs confirmation.

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ADDENDUM

After submission of this paper additional information came to hand which strongly supports the ideas put forward. Two Fremantle fishermen, the Poole Bros., brought into the W.A. Museum ten specimens of *Z. friendi* all trawled in 60 fms. W. of Dorre Is. (Shark Bay) in July, 1965. This is the most northerly confirmed record of the species. They are dark and in shape and dentition resemble other specimens from deep water north of Fremantle. Mean length of the series is 7.52 cm., range 6.82-8.23 cm. Mean W:L is 0.648, range 0.600-0.675. From dorsal view these shells would easily be mistaken for shallow water shells from Esperance, although they all possess the full series of crenulations along the columellar side so characteristic of northern populations.



PLATE 1. Dorsal views, approximately half natural size;

- (a) WAM 67-62, 25 fms., off False Entrance.
- (b) WAM 36-62, 2 fms., off Sorrento.
- (c) WAM 53-62, 2 fms., Parmelia Bank, Cockburn Sound.
- (d) WAM 39-62, 2 fms., Parmelia Bank, Cockburn Sound.
- (e) WAM 43-62, 2 fms., Parmelia Bank, Cockburn Sound.
- (f) WAM 24-63, 3 fms., off Quindalup, Geographe Bay.
- (g) WAM 1-62, 8 fms., off Quindalup, Geographe Bay.
- (h) WAM 28-63, 4 ft., Quindalup, Geographe Bay.
- (i) WAM 70-63, 3 fms., Esperance.
- (j) WAM 73-63, 3 fms., Esperance.
- (k) WAM 56-63, 3 fms., Esperance.
- (l) WAM N1996, ? fms., King George Sound.
- (m) WAM 61-62, 2 fms., Sir Joseph Banks Group, Spencer Gulf.



PLATE 2. Ventral views, approximately half natural size;

- (a) WAM 67-62, 25 fms., off False Entrance.
- (b) WAM 36-62, 2 fms., off Sorrento.
- (c) WAM 53-62, 2 fms., Parmelia Bank, Cockburn Sound.
- (d) WAM 28-63, 4 ft., Quindalup, Geographe Bay.
- (e) WAM 24-63, 3 fms., off Quindalup, Geographe Bay.
- (f) WAM 70-63, 3 fms., Esperance.
- (g) WAM 56-63, 3 fms., Esperance.
- (h) WAM 73-63, 3 fms., Esperance.
- (i) WAM N1996, ? fms., King George Sound.
- (j) WAM 61-62, 2 fms., Sir Joseph Banks Group, Spencer Gulf.

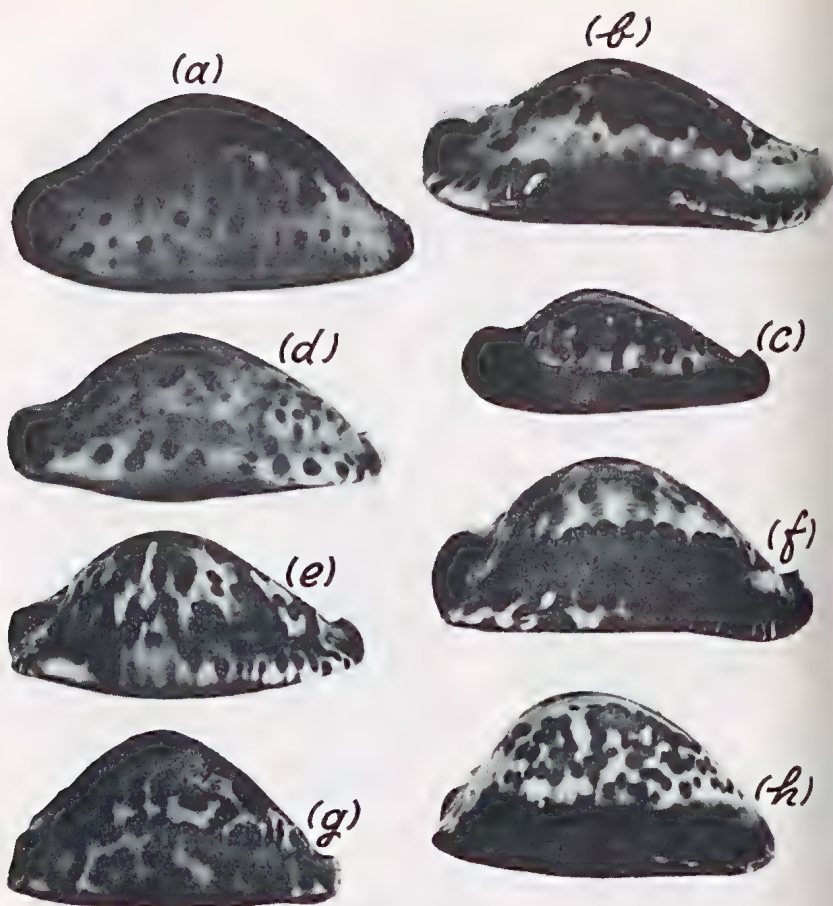


PLATE 3. Lateral views (right side), approximately half natural size;
 (a) WAM 67-62, 25 fms., False Entrance.
 (b) WAM 36-62, 2 fms., off Sorrento.
 (c) WAM 53-62, 2 fms., Parmelia Bank, Cockburn Sound.
 (d) WAM 24-63, 3 fms., off Quindalup, Geographe Bay.
 (e) WAM 1-62, 8 fms., off Quindalup, Geographe Bay.
 (f) WAM 70-63, 3 fms., Esperance.
 (g) WAM N1996, ? fms., King George Sound.
 (h) WAM 61-62, 2 fms., Sir Joseph Banks Group, Spencer Gulf.



PLATE 4. Dorsal, Ventral and Lateral views, approximately natural size, Lectotype of *Zoila thersites contraria* Iredale, A.M. C.35580, 72 fm., 60 m. W. of Eucla.

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